

Herbarium specimens shed light on the origins and flavour of early European tomatoes

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When the cultivated tomato (*Solanum lycopersicum* L.) was introduced to Europe in the 16th century it showed large variation in fruit colour, shape and size. However, the geographic origins of these tomatoes have long been debated and their flavour remains unknown. To address these questions, we sequenced 21 herbarium tomatoes collected in Europe between 1596 and 1915 and accessed 166 published sequences from 20th-century Latin American tomato varieties. Evolutionary genomic analyses showed that all historical specimens were most closely related to either large-fruited or cherry-sized modern tomatoes from Mexico, which suggests Mexico as the immediate origin of European tomatoes and is consistent with the variation in fruit size reported in historical records. Sequence variation at 119 genes related to fruit yield and flavour revealed haplotypes private to subsets of historical specimens at 13.3% of the flavour genes, but only at 5.7% of the fruit-yield genes. Across putative causal variants underlying fruit size and fruit flavour, specimens with a higher percentage of fruit-size increasing alleles tended to have a lower percentage of alleles associated with favourable flavour, consistent with genetic constraints underlying a trade-off between fruit size and flavour. Sequence variation at the fruit-sugar gene *LIN5* suggested that both historical and modern cherry-sized Mexican tomatoes are sweeter than their large-fruited counterparts. In contrast, variation at the *ALMT9* gene controlling malic acid metabolism suggested that historical large-fruited tomatoes might have tasted better than modern ones. These results highlight the potential of herbarium genomics to explore hidden stages of plant domestication.